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Genetic improvement of peanut in Argentina between 1948 and 2004: Links between phenology and grain yield determinants

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ABSTRACT

In the mid 1970s, there was a shift in peanut cultivars used in Argentina, from cultivars with erect growth habit (CEGH) to those with procumbent growth habit (CPGH), which improved seed yield, but also lengthened growth cycle. However, there is no information on (i) the partitioning of thermal time (TT) requirements between vegetative and reproductive phases, as well as between reproductive subphases representative of the seed set and seed-filling periods, and (ii) the effect of developmental changes on growth traits. Field experiments were performed to compute TT, grain yield determinants (i.e., seed number and seed weight), and other related physiological traits. Eight cultivars released between 1948 and 2004 were evaluated. The introduction of CPGH produced a lengthening (31%) of peanut growth cycle (S–R8), which was more pronounced for the reproductive phase (+39% for R1–R8) than for the vegetative phase (+17% for S–R1). This trend held for pod-set (R3–R6.5: +37%) and seed filling (R5–R8: +57%) subphases. It also held (CPGH > CEGH) for the rate of flower production (+80%), total flower number (+36%) and number of pods per plant (+117%), and consequently for the fertility index (+56%). The enhanced seed number of CPGH was related to ($r^2 = 0.55$, $P < 0.001$) the variation in crop growth rate during the seed set period ($CGR_{R3-R6.5}$), but not to the duration of this period. Variations in $CGR_{R3-R6.5}$ were partially explained by differences in cumulative IPAR, which were linked to the duration of the R3–R6.5 period as well as to maximum light interception fraction. These trends may have management as well as breeding origins. Introduction of the procumbent habit enhanced seed weight (CPGH > CEGH) and seed-filling duration markedly, but had no effect on seed-filling rate. Seed weight, however, was positively related to this rate ($P < 0.01$) and exhibited a negative trend in response to the duration of the period. Lack of source limitations on seed filling suggest that future breeding efforts should focus on the increase of seed numbers and the reduction of seed filling duration.

1. Introduction

Peanut (*Arachis hypogaea* L.) breeding in Argentina was initially based on cultivars of erect growth habit (CEGH); representative of the subpecies *fastigiata*. Grains of these cultivars met the demands of the oil industry; the main market for the species. Subsequently; changes in priorities led breeders to focus on new cultivars with enhanced yields and seed grade. As in most species for grain production; the former is commonly the primary objective of a breeding program (Evans, 1993); whereas the latter has been promoted by the peanut industry in the search of grain uniformity for direct human consumption (Holbrook and Stalker, 2003). In this context; the focus of Argentine peanut breeding during the 1970s changed toward the release of cultivars with procumbent growth habit (CPGH) of the subspecies *hypogaea* (Haro et al., 2013). An indirect trait related to these new cultivars was longer cycle than that of their predecessors. This change in crop development (i.e.; thermal time requirements for crop production) introduced in the evolution from CEGH to CPGH has been usually expressed by breeders in terms of calendar days; and represented a higher production risk due to a relatively short frost-free period in the main producing region of the country. An additional disadvantage

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Abbreviations: Exp, experiment; CGR, crop growth rate; CEGH, cultivars with erect growth habit; CPGH, cultivars with procumbent growth habit; FI, fertility index; PAR, photosynthetically active radiation; IPAR, incident PAR; fIPAR, fraction of IPAR intercepted by the crop; Rn, reproductive stage *n*; TT, thermal time.

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was the excessive development of canopies; both within and between the rows; which might contribute to the intensification of foliar and soilborne diseases (Tillman and Stalker, 2009).

Variations in thermal time (TT) requirements per se among cultivars of a given species do not imply changes in yield, except when these variations affect the physiological determinants of grain yield (e.g., crop or plant growth rates, seed set, seed growth). Such changes, therefore, may affect final grain yield depending on the ontogenic stage involved. For instance, a relative modification in the duration of pre-anthesis phases mediated by differences in photoperiod response may affect final grain number among wheat cultivars (Slafer et al., 2001), and further research demonstrated that these effects seemed mediated by changes in carbohydrate consumption that affect floret survival (Ghiglione et al., 2008). Similarly, research works in sunflower (Lopez Pereira et al., 1999), soybean (Kantolic et al., 2007) and maize (Capristo et al., 2007) crops detected that yield improvements were associated with a reduction in the pre-anthesis period and an increase in the duration of the anthesis-maturity period. In Argentine peanut genotypes, the duration of the whole growth cycle has been quantified, but there is no information on its partitioning along the cycle. Our first aim was to assess the partitioning of TT requirements between vegetative and reproductive phases, as well as between reproductive subphases representative of the critical windows of seed set and seed filling (Haro et al., 2008) in cultivars released in Argentina between 1948 and 2004. Our second aim was to identify the associations between these TT requirements and grain yield components (i.e., seed number and seed weight). We hypothesize that yield improvement among Argentine peanut cultivars released since 1948 has been mainly due to the lengthening of the seed set and seed weight phases, combined with mild improvements in source activity (i.e., plant and crop growth rates during these phases) partially evaluated in a previous paper (Haro et al., 2013).

2. Materials and methods

2.1. Experimental design and crop husbandry

Field experiments were conducted during the 2009–2010 (Exp1), 2010–2011 (Exp2 and Exp3) and 2011–2012 (Exp4) growing seasons at the research station of the National Institute of Agricultural Technology (INTA), located in Manfredi (31°49′S, 63°46′W), Córdoba province, Argentina. A detailed description of cultivars, crop husbandry and measurements can be found in Haro et al. (2013). Briefly, eight cultivars of contrasting growth habit developed for this region and released between 1948 and 2004 were sown on November 10 (Exp1), October 19 (Exp2), November 10 (Exp3) and November 1 (Exp4). This number of genotypes provided 90% coverage of farmer-adopted cultivars over the last 50 years (Haro et al., 2013). Exp1 and Exp2 were aimed at understanding breeding effects at the crop level; for this purpose, seeds were hand-planted at the row spacing (0.7 m apart) and stand density (14 plants m^{-2}) traditionally used by farmers. In these experiments, treatments (cultivars) were arranged in a completely randomized block design with three replicates; plots were four rows wide and 15 m long. Exp3 and Exp4 were performed to analyze traits at the individual plant level; plants were grown with almost no interference among them (ca. 1.5 m between individuals) and treatments were arranged in a completely randomized block design with five replicates (i.e., each experimental unit had one plant). The soil was a silty loam Typic Haplustoll (USDA Soil Taxonomy) and experiments received drip irrigation to keep the uppermost 1 m of the soil profile near field capacity throughout the growing season. Weeds and foliar diseases were adequately controlled.

Daily values of incident global solar radiation and mean air temperature were obtained from a weather station (LI-COR 1200, Lincoln, NE) installed at the experimental field. Solar radiation was converted into photosynthetically active radiation (PAR) by multiplying by 0.45 (Monteith, 1965), and accumulated TT was computed using mean daily air temperatures and a base temperature of 11 °C (Williams and Boote, 1995), from sowing (S) onwards.

2.2. Measurements

In Exp1 and Exp2, crop phenology (Boote, 1982) was observed on three plants tagged at R1 (first flower visible in at least 50% of the plants) in each plot. Light interception measurements and biomass sampling started at beginning pod (R3) and continued fortnightly. Light interception was assessed in each plot from 10 PAR measurements above the canopy ($\mathrm{IPAR_a}$) and 10 PAR measurements immediately below the lowest green leaves ($\mathrm{IPAR_b}$). Measurements were taken with a line-quantum sensor (AccuPAR radiometer; Decagon Devices, Inc., Pullman, WA) at between 1100 and 1400 h on clear days. For $\mathrm{IPAR_b}$ measurements, the sensor was fitted diagonally between the centers of two consecutive inter-row spaces. Fraction of IPAR (fIPAR) was computed as in the following equation:

$$\mathrm{fIPAR} = 1 - \left(\frac{\mathrm{IPAR_b}}{\mathrm{IPAR_a}}\right) \tag{1}$$

Values of fIPAR obtained with spot measurements performed at solar noon were adjusted for the diurnal variation in fIPAR using the relationship derived by Muchow (1985), which was previously applied in works on peanut (Bell et al., 1992; Haro et al., 2007). This correction was made to avoid the underestimation of IPAR computations at early stages of crop growth (Kemanian et al., 2004).

Shoot biomass was surveyed fortnightly between R1 and R8 (final harvest). For this purpose, plants within a 0.35 m^2 area of the two central rows were harvested, separated into leaves plus stems (vegetative biomass) and pods (reproductive biomass) when present, and dried at 70 °C until constant weight. Crop growth rate (CGR, in $g\,m^{-2}\,d^{-1}$) was estimated by linear interpolation for different periods along the cycle. At R8, total number of pods with seeds and total seed number were counted manually, and seeds were weighed for seed yield determination. The R8 stage was reached when 40% of the pods displayed a maturity darkening of the endocarp (Miller and Burns, 1971). Seed weight was computed as the quotient between seed yield and seed number. Seed filling rate (in $mg\,{}^{\circ}C\,d^{-1}$) during active seed filling was estimated as the quotient between final seed weight and the TT between R5 (beginning seed growth) and R8.

In Exp3 and Exp4, the numerical determinants of final seed number (flowers per plant, pods per plant and seeds per pod) were evaluated. The number of flowers per plant was surveyed daily between R1 and R8 (newly produced peanut flowers senesce in less than 24 h, and consequently do not cause a bias in successive counts), and a cumulative value computed during the same period. A trilinear with plateau model was fitted to the cumulative data (Eqs. (2)–(4)), which distinguishes three phases of flower production: (i) an early one at low rate (lag phase), (ii) a second one at maximum rate (phase of active flower production), and (iii) a third one where maximum flower number is reached and the rate is null.

$$\text{Total flower number} = a \times X, \quad \text{for} \quad X < b \tag{2}$$

$$\text{Total flower number} = (a \times b) + (c \times (X - b)), \quad \text{for} \quad d > X \geq b \tag{3}$$

$$\text{Total flower number} = (a \times b) + (c \times (d - b)), \quad \text{for} \quad X \geq d \tag{4}$$

where (i) b and d represent the start and end of the period of active flower production (in days after sowing), respectively, (ii) $(d - b)$ represents the duration of the period of active flower production (in days), and (iii) a (lag phase) and c (active phase) represent the daily rate of flower production (in flowers d^{-1}).

Table 1
Thermal time requirements of different developmental phases for cultivars released in Argentina between 1948 and 2004.

Growth habit	Cultivar	Thermal time requirements (°C day)				
		S–R8	S–R1	R1–R8	R3–R6.5	R5–R8
Erect	Colorado Manfredi	1216 b	364 b	829 c	365 b	452 b
	Blanco Santa Fe	1365 a	405 a	928 a	404 a	581 a
	Blanco Manfredi 68	1333 a	377 b	895 b	421 a	615 a
	Colorado Irradiado INTA	1209 b	370 b	823 c	368 b	463 b
	Mean	1281 B	379 B	868 B	389 B	528 B
Procumbent	Virginia 5 INTA	1697	455	1184	563	845 a
	Florman INTA	1684	432	1221	536	845 a
	ASEM 485 INTA	1673	443	1209	510	818 b
	ASEM 505 INTA	1667	437	1221	516	812 c
	Mean	1680 A	442 A	1209 A	531 A	830 A
	Year	0.0009	<0.0001	<0.0001	0.0333	NS
	Growth Habit (Cv)	<0.0001	0.0004	<0.0001	0.0001	<0.0001

Within each column, values followed by (i) different lowercase letters indicate differences among cultivars of the same growth habit group ($P < 0.05$), and (ii) different capital letters indicate differences between mean growth habit values ($P < 0.05$). NS: not significant.

The number of pods per plant was counted at R8, and a fertility index (i.e., pod set) was computed as the quotient between final pod number and final total flower number.

2.3. Statistical analyses

An analysis of variance (ANOVA) was performed to detect differences among cultivars for all evaluated traits, and breeding effects were estimated as the genetic gain for the attributes under study. This gain was computed as described in Haro et al. (2013). Linear models were fitted between variables by means of an optimization technique (Jandel Scientific, 1991). Significance of differences between the parameters of fitted linear models was evaluated using the F test (Statistix, 2000).

3. Results

3.1. Breeding effects on development

Duration of peanut growth cycle (in °C day) differed markedly between cultivars with contrasting growth habits (CPGH > CEGH; $P < 0.0001$, Table 1) and among CEGH ($P < 0.05$; Blanco Manfredi 68 and Blanco Santa Fe > Colorado Manfredi and Colorado Irradiado INTA). The change in growth habit introduced between 1973 and 1975 produced a mean increase of 40% in cycle duration of cultivar Virginia 5 INTA with respect to cultivar Colorado Irradiado INTA. Growth cycle values (averaged across years) ranged between 1209 and 1697 °C day (1.4-fold increase with respect to the minimum), with averages of 1281 °C day for CEGH and 1680 °C day for CPGH (Table 1). This difference between growth habits represented a 31% increase of the latter with respect to the former.

The mentioned differences in total cycle duration held for main vegetative and reproductive phases, as well as for sub-phases of the latter (Table 1). For the vegetative phase (sowing to R1), however, the longer duration detected among CPGH (mean value of 442 °C day) compared to CEGH (mean value of 379 °C day) represented only a 17% increase of this phase, and extreme values ranged between 364 and 455 °C day (1.25-fold increase with respect to the minimum). There were differences among CEGH ($P < 0.05$), but they were due exclusively to the longer vegetative phase of Blanco Santa Fe than that of the other erectophile cultivars (Table 1). Differences in cycle duration between growth habit groups increased for the reproductive phase (R1 to R8), which was 39% longer among CPGH (mean value of 1209 °C day) than among CEGH (mean value of 868 °C day). Extreme values ranged between 823 and 1221 °C day (1.48-fold increase with respect to the minimum), and the change in growth habit (year 1975) caused an increase of 44% in mean TT requirements of cultivar Virginia 5 INTA with respect to cultivar Colorado Irradiado INTA. Significant differences ($P < 0.01$) in the duration of this broad reproductive phase were also detected among CEGH (Blanco Santa Fe > Blanco Manfredi 68 > Colorado Manfredi and Colorado Irradiado INTA). As a result of these trends, the percent distribution of the cycle between the vegetative phase (S–R1) and the reproductive phase (R1–R8) resulted in a decrease of the former (−3.6%) and an equivalent increase of the latter with the shift from CEGH (30.4% for S–R1 and 69.6% for R1–R8) to CPGH (26.8% for S–R1 and 73.2% for R1–R8).

The trends described for the R1–R8 phase were also evident for the reproductive sub-phases of R3–R6.5 (pod-set period) and R5–R8 (seed-filling period). The former increased 53% with the change in growth habit between 1973 and 1975. The duration of this sub-phase ranged between 365 and 563 °C day (1.54-fold increase with respect to the minimum), with mean values of 389 and 531 °C day for CEGH and CPGH (Table 1), respectively (i.e., 37% increase of the latter with respect to the former). There were differences for this trait among CEGH ($P < 0.05$; Blanco Santa Fe and Blanco Manfredi 68 > Colorado Manfredi and Colorado Irradiado INTA), but there was no clear trend related to breeding effects other than the mentioned differences between growth habit groups (Table 1). The introduction of the procumbent growth habit caused the described increase in duration of the pod-set period, which was partially offset by subsequent negative breeding effects (−1.73 °C day y^{-1} since 1975; $P < 0.05$). The variations observed in the seed-filling phase were similar to those detected for the seed-set period. For the last phase of the cycle (R5–R8), which partially overlaps the seed-set phase, we detected (i) a marked increase in duration (83%) caused by the introduction of the procumbent habit, (ii) a large range between minimum (452 °C day) and maximum (845 °C day) values (1.87-fold increase with respect to minimum), (iii) a significant difference between mean values of contrasting growth habits ($P < 0.0001$, Table 1), which reached 528 °C day for CEGH and 830 °C day for CPGH (i.e., 57% increase of the latter with respect to the former), (iv) significant differences among CEGH ($P < 0.01$; Blanco Santa Fe and Blanco Manfredi 68 > Colorado Manfredi and Colorado Irradiado INTA) and CPGH ($P \leq 0.001$; Virginia 5 INTA and Florman INTA > ASEM 485 INTA > ASEM 505 INTA), and (v) a lack of breeding effects among CEGH but a significant ($P < 0.001$) and negative effect among CPGH (−1.22 °C day y^{-1}, equivalent to −0.15% y^{-1}).

The differences described in total cycle duration (S–R8) were significantly and positively related to variations detected in all evaluated phases, but the established relationships were stronger for the reproductive phase ($r^2 = 0.97$, $P < 0.001$) and its sub-phases ($r^2 \geq 0.91$, $P < 0.001$) than for the vegetative phase. A single linear model always gave a good fit to the whole data set (Cultivars × Exp), except for the relationship between TT_{S-R8} and TT_{S-R1}. In this case,

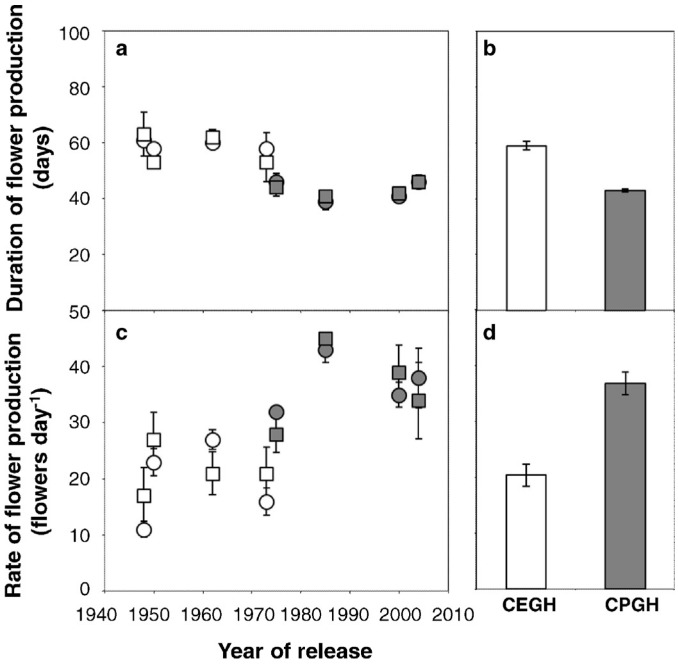

Fig. 1. Evolution of the (a) duration of active flower production, and (c) active rate of flower production of peanut cultivars released in Argentina between 1948 and 2004. Average (b) duration of active flower production and (d) active rate of flower production of cultivars with erect (CEGH) and procumbent (CPGH) growth habit. In (a) and (c), CEGH in white symbols, and CPGH in gray symbols. Exp. 3: circles, Exp. 4: squares. Bars are the standard error of the mean.

two models were necessary to capture a significant ($P < 0.001$) year effect ($r^2 = 0.93$ for Exp1 and $r^2 = 0.84$ for Exp2). Delayed sowing of Exp1 had no effect on the slope of the relationship (5.4 for Exp1 and 5.8 for Exp2–unitless-) but had a significant effect on the ordinate (−991 for Exp1 and −628 for Exp2), which represented a 74.7 °C day increase in the duration of the vegetative phase, as compared to Exp2.

3.2. Breeding effects on the physiological determinants of pod set and final seed number

Breeding caused (i) a decrease in the duration of active flower production (Fig. 1a and b), and (ii) an increase in the active rate of flower production (Fig. 1c and d). These trends were exclusively associated with the shift from CEGH to CPGH. Introduction of the procumbent growth habit represented a shortening of 20% in the extension of the mentioned period. Values (averaged for each cultivar across years) ranged between 40 and 62 days (i.e., 1.55-fold increase with respect to the minimum), and mean values of 59 and 43 days were computed for CEGH and CPGH (Fig. 1b), respectively (i.e., 27% decrease of the latter with respect to the former). For the rate, however, it was a 2-step response, with a first 61% increase driven by the introduction of the procumbent Virginia 5 INTA in 1975, and a subsequent 33% increase promoted by the release of Florman INTA in 1985. Values (averaged for each cultivar across years) ranged between 14 and 44 flowers d^{-1} (3.14-fold increase with respect to the minimum), and mean values of 20 and 37 flowers d^{-1} were computed for CEGH and CPGH (Fig. 1d), respectively (i.e., 85% increase of the latter with respect to the former). These traits had no additional response to breeding (i.e., no trend across YOR).

Total flower number was negatively related to the duration of active flower production (Fig. 2a) and positively related to the active rate of flower production (Fig. 2b). In spite of this opposite trend, total flower number increased with the introduction of the

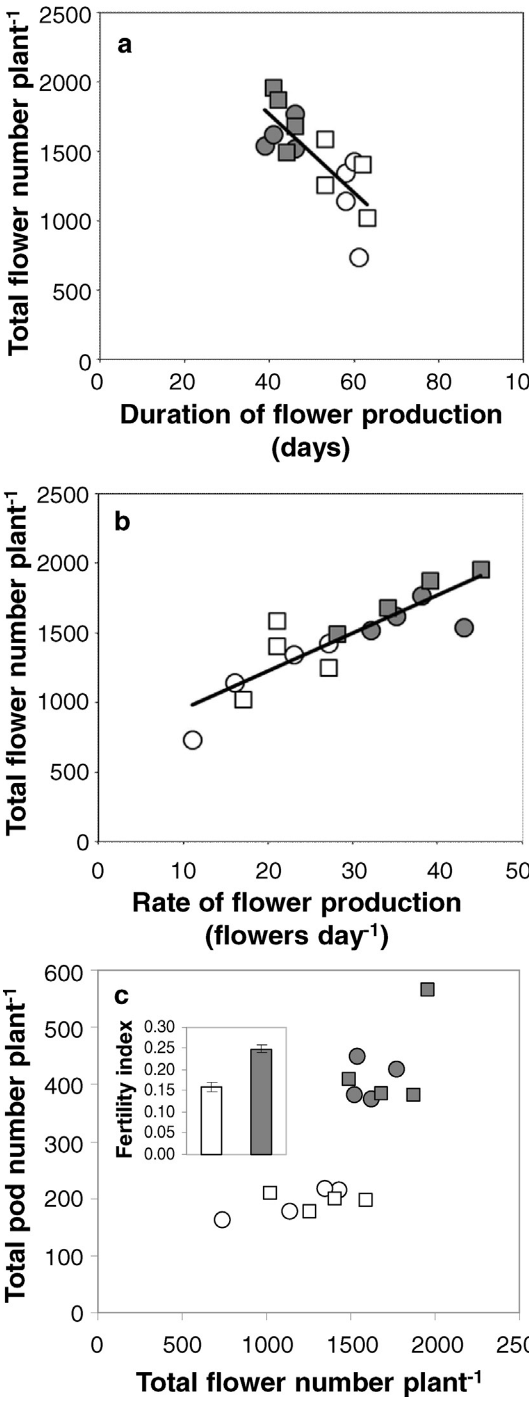

Fig. 2. Response of total flower number per plant to (a) duration of active flower production ($Y = 2898 - 28.2X$, $r^2 = 0.59$, $P < 0.001$), and (b) active rate of flower production ($Y = 683 + 27.3X$, $r^2 = 0.75$, $P < 0.001$). In (c), the response of total pod number per plant to total flower number per plant. Each symbol represents a cultivar mean ($n = 5$). Symbols as in Fig. 1. The inset in (c) represents the fertility index of CEGH (white) and CPGH (gray).

procumbent habit (CPGH > CEGH; $P < 0.01$). Growth habit had the same effect on the number of pods per plant (CPGH > CEGH; $P < 0.01$), and caused a clustering of data in the response of this trait to total flower number (Fig. 2c). Mean values of pod set (fertility index = pods per developed flower) were 0.16 for CEGH and 0.25 for CPGH (Fig. 2c, inset).

Seed number m^{-2} was strongly related to pod number m^{-2} ($r^2 \geq 0.87$) and both traits had no clear response to the duration of the R3–R6.5 period. The procumbent group always had a

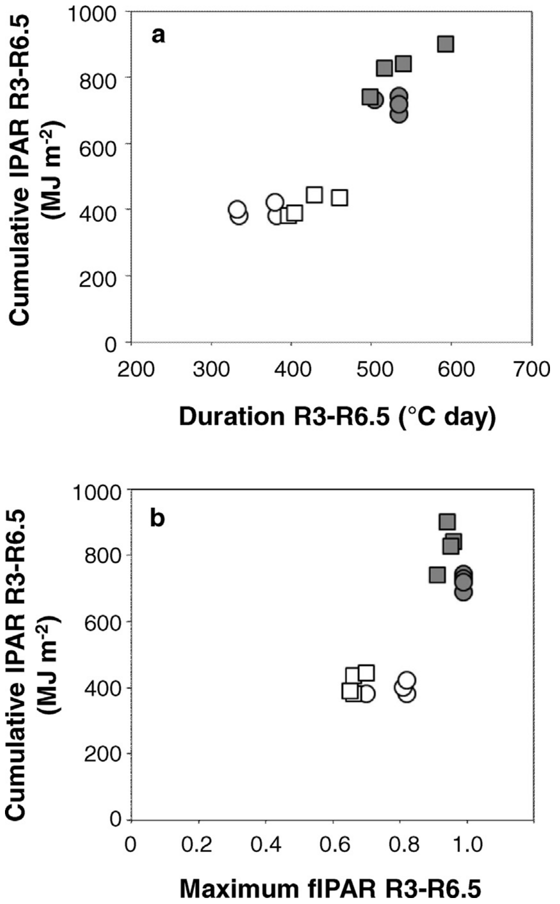

Fig. 3. Response of cumulative IPAR during R3–R6.5 to (a) the duration of the R3–R6.5 period, and (b) maximum fIPAR during R3–R6.5. Each symbol represents a cultivar mean ($n = 3$). Symbols as in Fig. 1.

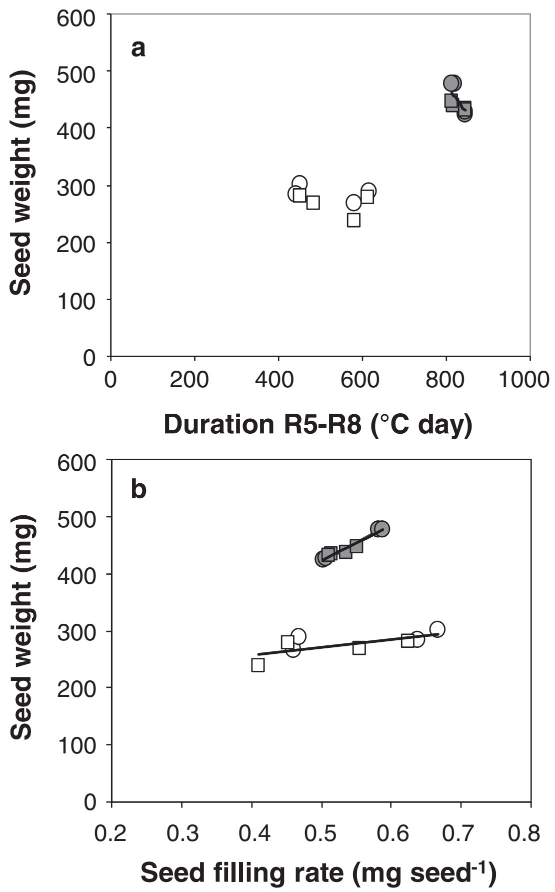

Fig. 4. Response of seed weight to (a) the duration, and (b) the rate of seed filling during the R5–R8 period. Each symbol represents a cultivar mean ($n = 3$). Symbols as in Fig. 1. Solid lines represent models fitted to each growth habit group, in (a) $Y = 1255 - 0.98X$, $r^2 = 0.53$, $P < 0.05$ for CPGH, and (b) $Y = 206 + 130X$, $r^2 = 0.47$, $P < 0.10$ for CEGH; $Y = 116 + 614X$, $r^2 = 0.96$, $P < 0.001$ for CPGH.

higher seed number (range 978–1134 seeds m^{-2}) than the erect one (range 867–1031 seeds m^{-2}). Contrary, a significant quadratic model ($r^2 = 0.55$, $P < 0.001$) was fitted to the response of seed number m^{-2} to crop growth rate during the seed set period ($\text{CGR}_{\text{R3–R6.5}}$). This model had a zero intercept ($Y = 103.34X - 2.36X^2$), and CPGH had larger $\text{CGR}_{\text{R3–R6.5}}$ values (mean = 15.6 ± 0.7 g m^{-2} d^{-1}) than CEGH (mean $\text{CGR}_{\text{R3–R6.5}}$ = 13.9 ± 0.5 g m^{-2} d^{-1}).

The variation recorded in $\text{CGR}_{\text{R3–R6.5}}$ across cultivars and years was partially explained by the variation observed among computed values of cumulative IPAR during the same period ($r^2 = 0.25$, $P = 0.04$, $n = 16$). For the latter, mean values ranged between 408 MJ m^{-2} for CEGH and 776 MJ m^{-2} for CPGH (i.e., 90% increase of the latter with respect to the former). Differences in cumulative IPAR were linked to differences between growth habit groups (CPGH > CEGH) in (i) duration of the R3–R6.5 period (Table 1, Fig. 3a), and (ii) maximum light interception fraction (fIPAR) during the R3–R6.5 period (Table 2, Fig. 3b), which reached 0.75 for CEGH and 0.97 for CPGH. Differences in mean values of fIPAR represented an increase of 29% for CPGH with respect to CEGH. No additional breeding effect was detected for traits related to light capture within each growth habit group.

3.3. Breeding effects on the physiological determinants of seed weight

The introduction of the procumbent habit had a marked effect on seed weight and seed-filling duration (Fig. 4a), but not on seed-filling rate (Fig. 4b). Mean values of seed weight and seed-filling duration were always higher for CPGH (445 ± 7.6 mg seed^{-1} and 830 ± 5.7 °C day, respectively) than for CEGH (276 ± 6.7 mg seed^{-1} and 528 ± 27.2 °C day, respectively). A clear clustering of data was evident for the duration of seed filling (Fig. 4a), with CPGH having always higher values than CEGH. The proportion of change in this trait produced by the procumbent habit was high (57% increase for CPGH as compared to CEGH), and almost matched the mean increase in seed weight (61% for CPGH as compared to CEGH). Contrary, for the rate of seed filling we recorded a large overlapping of values among cultivars of both growth habit groups (Fig. 4b). Within each group, however, observed variations in seed weight were better explained by variations in the rate ($r^2 = 0.47$ for CEGH, $P < 0.05$; $r^2 = 0.96$ for CPGH, $P < 0.001$) than by variations in duration ($r^2 = 0.15$ for CEGH, ns; $r^2 = 0.53$ for CPGH, $P < 0.05$) of seed filling. Moreover, the relationship was always positive for the former (Fig. 4b) and negative for the latter (Fig. 4a), and a strong ($r^2 \geq 0.72$, $P < 0.01$) negative relationship was established between rate and duration of seed filling for both groups. For the rate, we estimated a significant ($P < 0.01$) genetic gain of 0.0023 mg °C day^{-1} y^{-1} (0.43% y^{-1}) only among CPGH. Crop growth rate (Table 2) and the source-sink ratio during active seed filling (i.e., quotient between crop growth between R5 and R8 and final seed number; Haro et al., 2013) had no effect on the physiological determinants of seed weight.

4. Discussion

Peanut grain yield depends upon the aptitude of a variety to mature a reasonable number of fruits during the available

Table 2
Effect of treatments on maximum light interception efficiency (fIPAR) during the R3–R6.5 period, the amount of IPAR accumulated during the R3–R6.5 and R5–R8 periods, and crop growth rate (CGR) during these same periods.

Growth habit	Cultivar	Maximum fIPAR	Cumulative IPAR ($\mathrm{MJ\,m^{-2}}$)		CGR ($\mathrm{g\,m^{-2}\,d^{-1}}$)	
		R3–R6.5	R3–R6.5	R5–R8	R3–R6.5	R5–R8
Erect	Colorado Manfredi	0.74	383	598	14.3	11.7
	Blanco Santa Fe	0.76	435	833	12.5	10.8
	Blanco Manfredi 68	0.75	411	639	14.3	9.9
	Colorado Irradiado INTA	0.73	398	578	14.7	11.4
	Mean	0.75 B	408 B	662 B	13.9	10.9
Procumbent	Virginia 5 INTA	0.97	824	1489	14.2	10.4
	Florman INTA	0.98	768	1491	14.7	11.4
	ASEM 485 INTA	0.95	782	1477	16.5	13.5
	ASEM 505 INTA	0.97	731	1411	17.2	12.2
	Mean	0.97 A	776 A	1467 A	15.6	11.8
	Year	0.0031	0.0331	0.0011	NS	NS
	Growth Habit (Cv)	<0.0001	<0.0001	<0.0001	NS	NS

Within each column, values followed by different capital letters indicate significant differences ($P < 0.05$) between mean growth habit values. NS: not significant.

seed-filling phase. Therefore, phenological fitness is a priority objective in many plant breeding programs of this species (Ndoye, 1988; Vasudeva Rao et al., 1992). Earliness reduces the duration of crop risk mainly under unfavorable environmental conditions, and provides an enhanced flexibility in planting time within growing seasons (Ndoye, 1988). These characteristics were represented by CEGH (subspecies *fastigiata*) during the first decades of peanut breeding in Argentina, where the crop cycle of late-maturing cultivars may be limited by frosts before harvest. The strategy of selection for early-maturing crops produced mean yields of $271\ \mathrm{g\,m^{-2}}$ in a period of ca. 130 days (1281 ± 30 °C day). Since 1975, strong yield increases have been obtained with the introduction of CPGH (subspecies *hypogaea*), and a genetic gain of $2.01\ \mathrm{g\,m^{-2}\,y^{-1}}$ (mean genetic gain of $0.43\%\ \mathrm{y^{-1}}$) was estimated for the 1975–2004 period (Haro et al., 2013). This increase in yield, however, has been accompanied by a lengthening in growth cycle, which was estimated as a mean increase of 31% among CPGH with respect to CEGH. Enhanced seed yield obtained with the introduction of large-seeded runner types released since the middle of the 1970s was accompanied by an increased in seed grades (Haro et al., 2013). This trend had the additional benefit of an improved income for Argentine peanut growers, because product price varies with a quality trait based on seed grade (Mozingo et al., 1987). In the current study we found that this lengthening in growth cycle was mainly due to increases in reproductive stages (i.e., from R1 onwards), because the vegetative phase that elapses between sowing and the start of flowering (R1) did not augment markedly (increase of 16.5% in CPGH with respect to CEGH). On the one hand, these responses are in contrast with evidences reported for other summer-cropped species, in which the average duration of the growth cycle was reduced by breeding effects, and such reduction was a consequence of a shortening in the time to anthesis with almost no change in the duration of the period between anthesis and maturity (Evans, 1993; Lopez Pereira et al., 1999; Russell, 1991). On the other hand, the overall final result does match the trend of most crops, because it increased the proportion of the reproductive phases with respect to the vegetative phase.

In peanut, the flowering phase may span most part of the cycle, but the sub-phase between R1 and R3 is the reproductive period that defines the potential number of seeds. Seed set takes place at subsequent stages (i.e., pegging, beginning of pod and seed growth) and defines the actual number of seeds at harvest. Introduction of the procumbent habit in Argentina caused an increase in total flower numbers, because the observed reduction in the duration of the flowering period was over-compensated by the increase registered in the rate of flower production. These trends were accompanied by a strong increase in the number of pods that reached maturity among CPGH, with positive consequences on the fertility index (FI) computed for isolated plants (i.e., potential values). Mentioned breeding effects on rate and duration of flower production may have synchronized the flowering-pollination-fertilization process among flowers, which is expected to improve pod set (Egli and Bruening, 2002b) due to the benefit of a reduced competition for assimilates between early and late developing pods (Egli and Bruening, 2002a).

The FI calculated in current work underlined the high levels of flower abortion and low efficiency of pod set in peanut crops ($\mathrm{FI} \leq 0.29$), as documented in previous studies that used shading during the pegging and podding phases (Hang et al., 1984), high temperatures during flowering (Vara Prasad et al., 1998, 1999a, 1999b, 2000), water stress (Harris et al., 1988; Nageswara Rao et al., 1985; Pallas et al., 1979) and impaired pegging (Collino et al., 2001; Haro et al., 2008, 2010, 2011). Coffelt et al. (1989) estimated the FI in 14 cultivars with contrasting growth habits using different computations methods, and one of them (described as REM2) matched our computation system (i.e., quotient between final pod number and total number of flowers). Their general results (the FI ranged between 0.18 and 0.35, and averaged 0.25) are in good agreement with our findings (FI between 0.14 and 0.29, average of 0.21), but the trend between growth habit groups was the opposite. They found higher indices among CEGH (mean value of 0.28) than among CPGH (mean value of 0.22), in disagreement with our results (means of 0.16 for CEGH and 0.25 for CPGH). Coffelt et al. (1989) suggested that increases in the FI of early maturing cultivars of erectophyle habit may have resulted from higher partition of assimilates to the reproductive structures than to the vegetative structures with respect to late maturing cultivars of spreading (procumbent) habit. There are, however, some additional aspects that deserve attention for correct comparisons. First, contrasting trends cannot be attributed to the difference in flower numbers between growth habit groups, which was estimated as 63% larger for CPGH as compared to CEGH in their study and 54% larger for the same comparison in our work. By contrast, final pod numbers were only 27% higher for CPGH than for CEGH in their study and 245% higher for the same comparison in our work. This large difference may be mostly attributed to differences in measurement techniques; indeed, we measured isolated plants whereas Coffelt et al. (1989) measured plants grown at regular stand densities, because we detected no difference in seed numbers (equivalent to ca. twice the number of pods) between group habits for crops grown at normal densities in Exp1 and Exp2 (Haro et al., 2013). In other words, FIs cannot be appropriately compared when data are collected at very contrasting stand densities, because flower and pod (or seed) numbers usually have a different response to crowding (Donald, 1954; Otegui, 1997). Second, attention should be paid to differences derived from contrasting genotype × environment effects in each study. For instance, a similar sowing date was used in Coffelt et al. (1989) and our work (early May in the northern hemisphere is equivalent to early November in the southern hemisphere), but differences in latitude (ca. 36°42′N in the US and ca. 31°49′S in Argentina) combined with differences in cycle duration across genotypes (not specified in their work) may have represented an important variation in the photothermal environment (Cantagallo et al., 1997; Fischer, 1985) during pod set, and added an extra bias for adequate comparisons.

The release of cultivar Virginia 5 INTA (first procumbent cultivar) produced a 52% yield increase with respect to cultivar Colorado Irradiado INTA (last erect cultivar) (Haro et al., 2013), but was accompanied by a pronounced lengthening of the crop cycle (40%) with the already described increase in production risk due to early frosts. Consequently, shortening of the growth cycle without yield penalty became a priority for Argentine breeding programs, and subsequent genotypes showed a gradual reduction in TT requirements ($-1.73\,^{\circ}\mathrm{C}\ \mathrm{day}\,\mathrm{y}^{-1}$) for the seed set period (R3–R6.5). This trend had no negative effect on the number of seeds, and the sink size (i.e., seed number m^{-2}) did not decrease. This was probably due to compensatory effects in the source of assimilates (e.g., increased CGR) during the mentioned period (Jogloy et al., 2011). Breeding did not cause a clear effect on $\mathrm{CGR}_{\mathrm{R3-R6.5}}$, but this trend does not mean a null effect of $\mathrm{CGR}_{\mathrm{R3-R6.5}}$ on seed number. Contrary, Haro et al. (2013) demonstrated that seed number was significantly ($P < 0.001$) related to CGR during the R3–R6.5 phase. In our work, $\mathrm{CGR}_{\mathrm{R3-R6.5}}$ was larger among CPGH than among CEGH, and this trend was in part explained by traits that enhanced light capture. Consequently, management practices that alter light distribution through the canopy, such as plant density (Bell and Wright, 1998) and row spacing (Colvin et al., 1985; Cox and Reid, 1965), can affect the final result of the crop, regardless of the growth habit of cultivars. Accordingly, our results suggest that the reduced yield recorded among CEGH could have been due not only to positive breeding effects related to the procumbent habit but also to the combination of low stand density and wide inter-row spacing, which hindered maximum light interception during pod set. In other words, traditional levels of stand density (14 plants m^{-2}) and row spacing (0.7 m between rows) used by farmers may have represented a penalty for CEGH that was compensated by the spreading characteristic of the procumbent group. This type of genotype × management responses has been documented for other crops, such as maize (Duvick, 2005; Luque et al., 2006) and soybean (Cooper, 1977; Duncan, 1986; Egli, 1976; Ikeda, 1992), particularly in relation to density-dependent responses.

Haro et al. (2013) demonstrated that improved seed yield caused by peanut breeding in Argentina was mainly driven by an increase in seed weight than by the increase in seed numbers. Increasing seed weight was a goal of local breeders to satisfy industry requirements (Mozingo et al., 1987), and was achieved with the introduction of large-seeded runner types (CPGH > CEGH). This trend translated directly into enhanced seed yield because of excess source availability during seed filling, which avoided any possible trade-off between seed yield components (Haro et al., 2013). Besides seed size, procumbent cultivars produced the already mentioned cycle lengthening, particularly of the R5–R8 period (82.5% increase between 1973 and 1975). Our analyses suggest that (i) breeding caused a simultaneous increase in seed weight and seed filling duration and did not modify the rate of seed filling between growth habit groups, and (ii) within each group, seed weight has a positive response to the filling rate and a negative one to the duration. These findings are in agreement with similar studies in peanut (Duncan et al., 1978) and other summer crops such as soybean (Liu et al., 2005) and maize (Russell, 1985; Tollenaar, 1989) grown in environments where the frost-free period sets a limit to resource use and final attainable grain yields (Cavalieri and Smith, 1985; Crosbie, 1982; Meghji et al., 1984; Russell, 1985). Delayed seed filling tends to reduce the percentage of pods that reached full maturity, and for this reason subsequent breeding efforts should aim to (i) shortening this reproductive subperiod, and (ii) minimizing the negative effects of this shortening on resource use for adequate seed filling. Shortening was achieved at a rate of $-1.22\,^{\circ}\mathrm{C}\ \mathrm{day}\,\mathrm{y}^{-1}$ during the last 30 years. Regarding minimizing negative effects, reductions in duration ($-0.15\%\,\mathrm{y}^{-1}$) had been largely compensated by a steady increase in seed filling rate ($0.43\%\,\mathrm{y}^{-1}$), as proposed by Seaton et al. (1992). Up to the present, these trends had no negative effect on final grain yield, and estimates of the source-sink ratio during seed filling (Haro et al., 2013) suggested that Argentine peanut crops are not source-limited during this period.

5. Conclusions

This study is the first one to quantify TT requirements for the vegetative and reproductive phases, as well as reproductive subphases (representative of the critical windows of seed set and seed filling) of peanut cultivars released between 1948 and 2004 in Argentina. Increases in peanut yield were obtained with the introduction of CPGH, which involved lengthening of the growth cycle, chiefly of the reproductive stages. Increases in the rate of flower production compensated the shortening of the active flowering period among CPGH, producing an increase in total flower number and a strong increase in the number of pods for this group. These trends had a positive consequence on the FI. Introduction of the first CPGH (Virginia 5 INTA) caused a lengthening of the R3–R6.5 period, but subsequent cultivars experienced a gradual reduction in TT requirements of this stage without negative effects on seed number. CPGH showed increases in $\mathrm{CGR}_{\mathrm{R3-R6.5}}$ that were partially explained by enhanced light capture. This trend, however, cannot be attributed exclusively to breeding effects, and subsequent experiments should include an alternative combination of enhanced stand density and/or reduced row spacing for the correct evaluation of breeding and management sources of variation. Introduction of the procumbent habit caused a drastic increase in seed weight and seed filling duration but not on the rate of seed filling. Within each growth habit group, however, seed weight is negatively related to the duration of the R5–R8 phase and positively related to the rate of the filling process. Results suggest that future breeding efforts should focus on increasing seed numbers and reducing seed filling duration, because current source availability during seed filling is not setting a limit to final seed yield.

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